FIGURES 1–4. Graphic representation of the distribution of long- and short-styled forms represented by herbarium collections, together with histogram distribution of the stamen numbers. FIG. 1, *Saurauia tomentosa* (H.B.K.) Spreng.; FIG. 2, *S. omichlophila* R. E. Schult.; FIG. 3, *S. putumayonis* R. E. Schult.; FIG. 4, *S. ursina* Tr. & Pl. Sample examined for each species consists of short- and long-styled forms in more or less equal numbers.

rauia bullosa Wawra, *S. brachybotrys* Turczaninow, *S. excelsa* Willdenow, *S. Humboldtiana* Buscalioni, *S. tomentosa* (H.B.K.) Sprengel, *S. omichlophila* R. E. Schultes, *S. putumayonis* R. E. Schultes, and *S. ursina* Triana & Planchon. Data for each species, such as presented in TABLE 1 for *S. bullosa*, and in TABLE 2 for *S. omichlophila*, have been converted into graphs, FIGS. 1–8. Of the eight species, seven show a definite correlation between low pollen fertility (or absolute pollen sterility and a long-
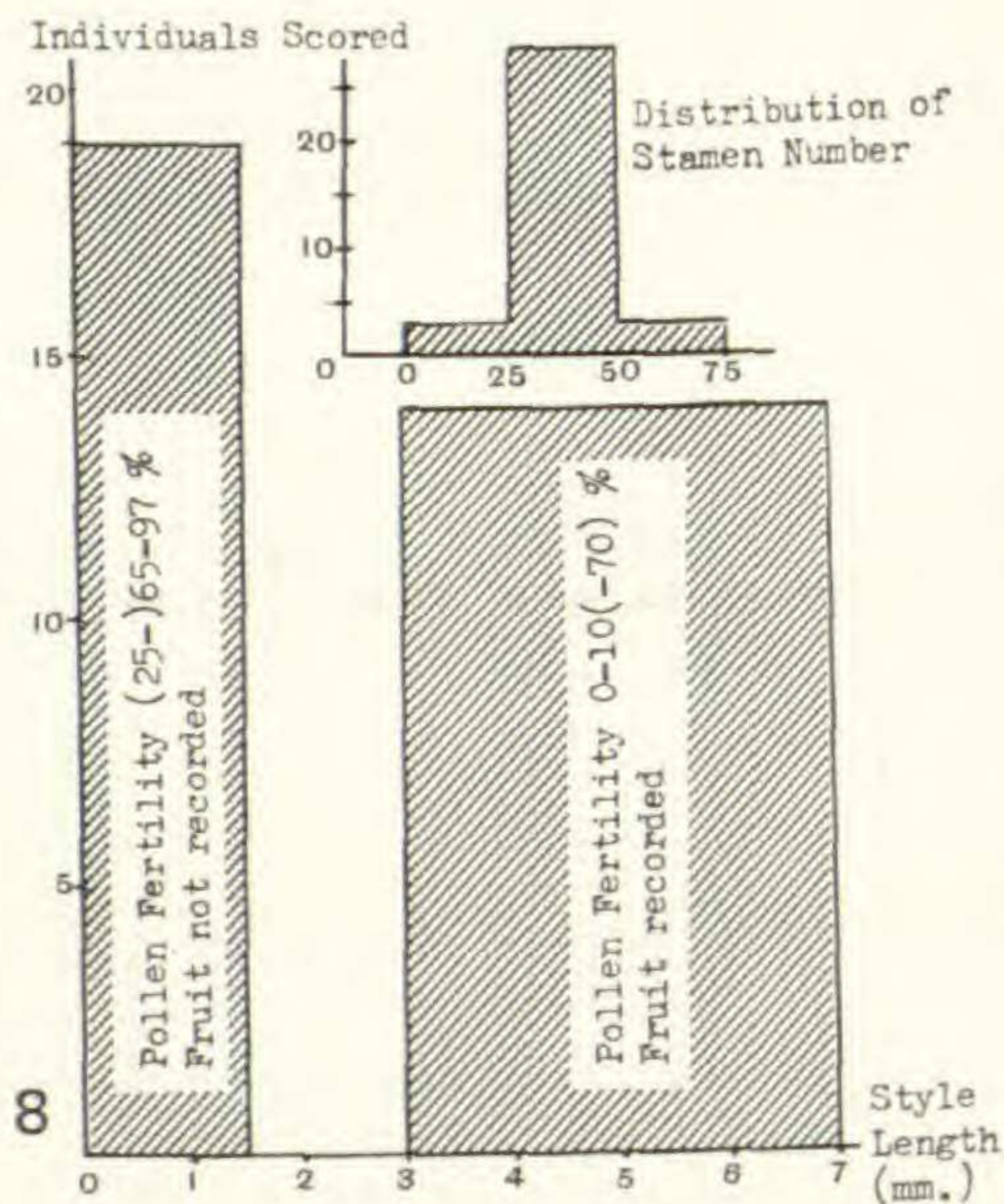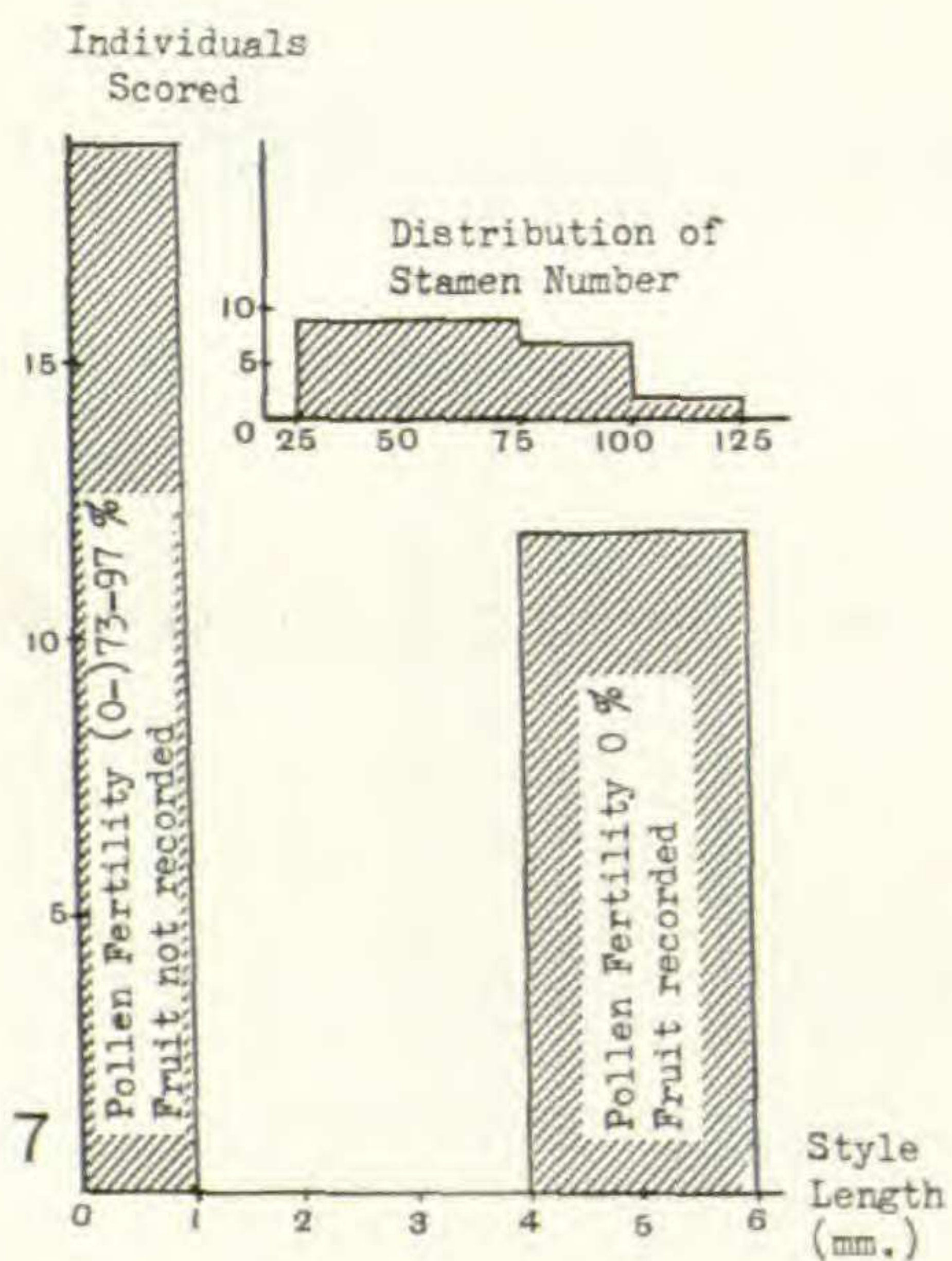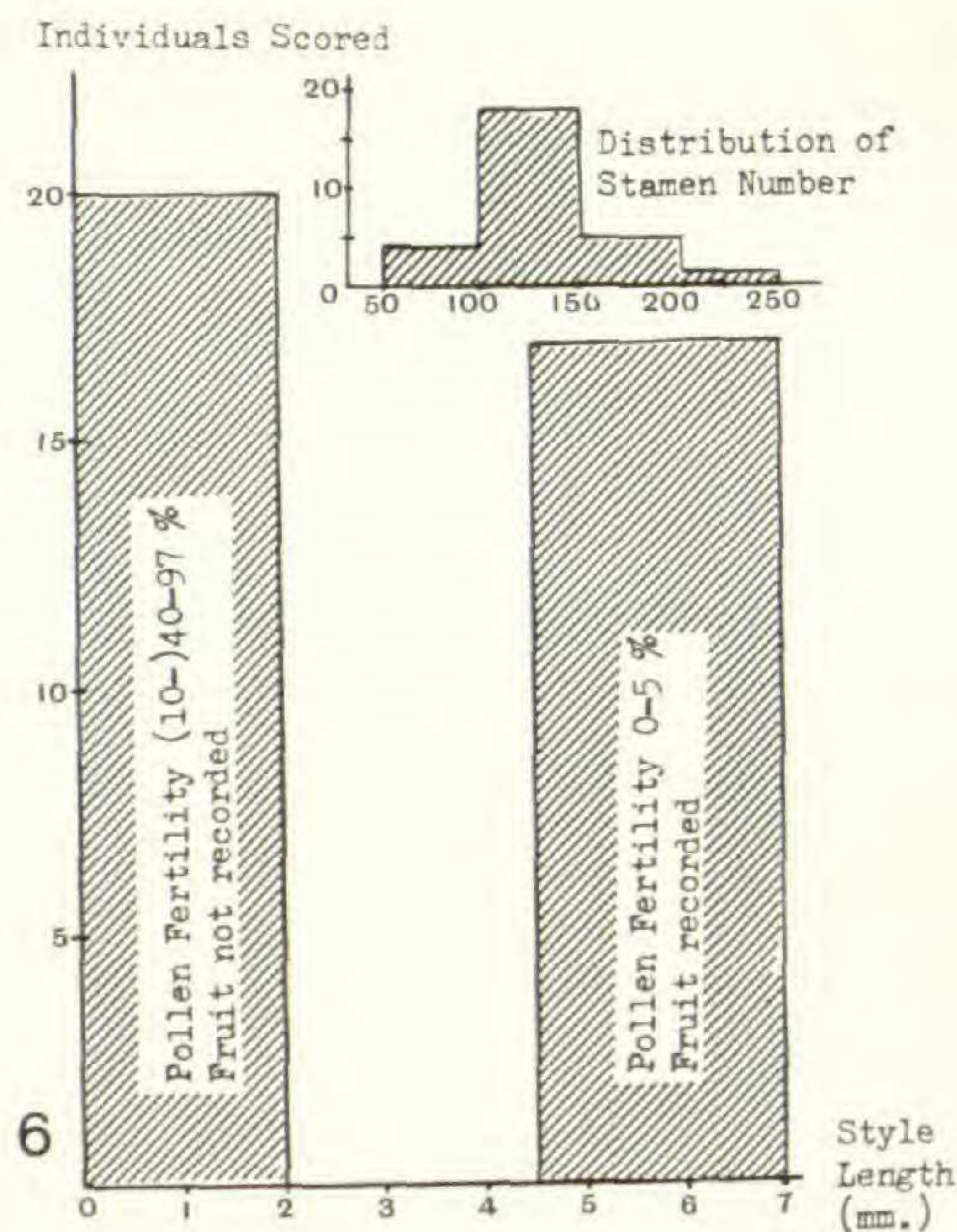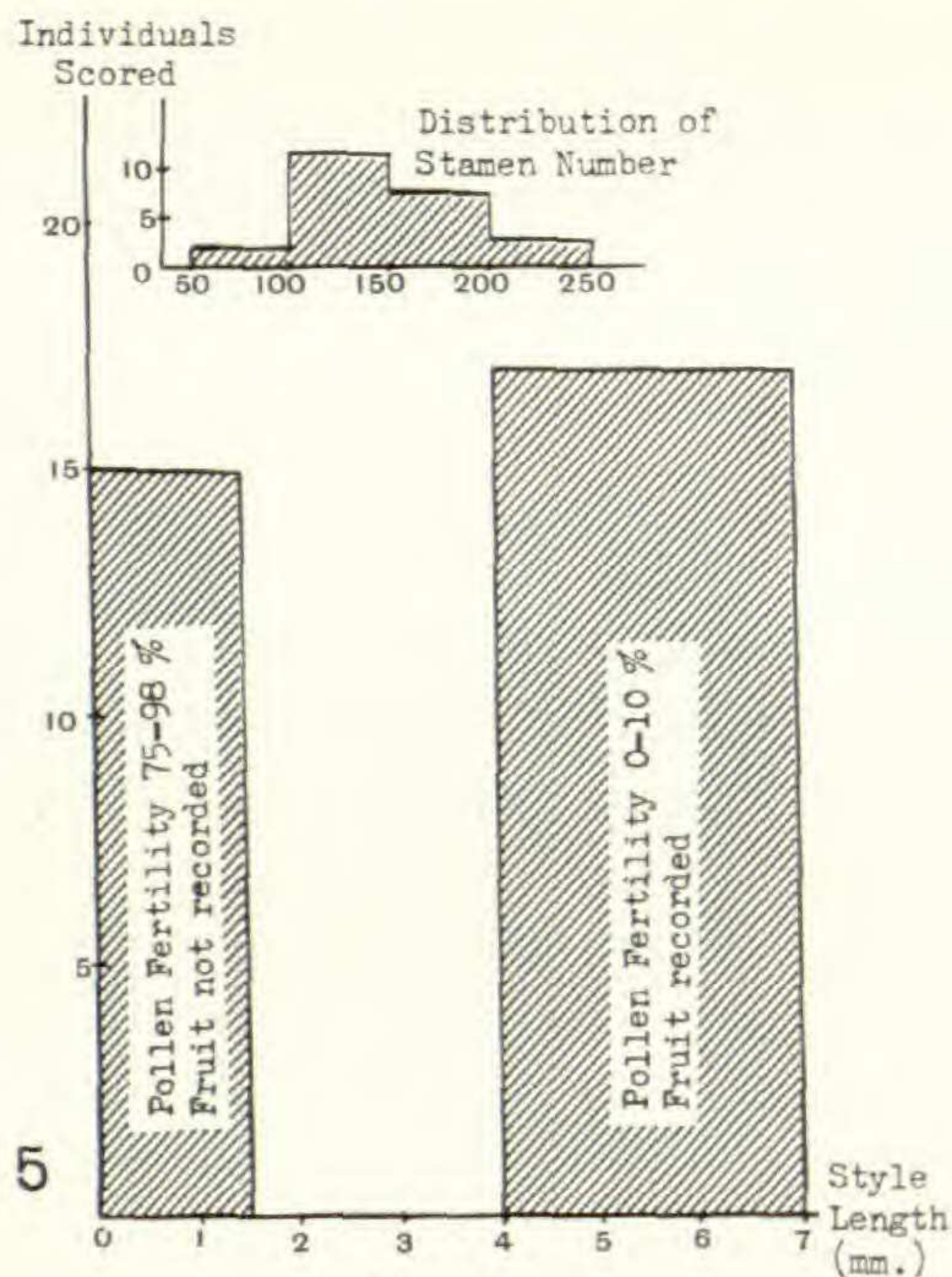
Table 1. Saurauia bullosa Wawra

Collector	Fl. buds or Fls.	Pollen Fertility (%)	Style Length (mm.)	Stamen Number	Fruit	Collecting Date	Altitude (m.)
Soejarto 496	—	—	5.5	—	+	Aug.	2900
Soejarto 1504	—	—	6	—	+	Aug.	3000
Soejarto 1533	—	—	6.5	—	+	Aug.	2700
Soejarto 1472	+	0	5	160	—	Aug.	3100
Soejarto 1336	—	—	7	—	+	Aug.	2900
Soejarto 495	+	0	6	115	+	Aug.	2900
Soejarto 1015	+	0	5	127	+	July	3200
Soejarto 1478	+	0	5.5	220	—	Aug.	2900
Soejarto 1595	+	0	7	160	—	Sept.	3000
Soejarto 500	+	0	5	125	—	Aug.	2900
Cuatrecasas 20805	+	0	6	100	+	Apr.	3100
Cuatrecasas 20414	+	1	4.5	85	—	March	3200
Cuatrecasas 23316	+	2	5	70	—	Nov.	3000
Jorge Castro 78	+	0	5	140	—	Apr.	3400
L. Uribe Uribe 5278	+	0	5.5	100	+	July	3000
Ynes Mexia 7599	+	10	5	140	—	Aug.	3000
Soejarto 1496	+	75	0	175	—	Aug.	3100
Soejarto 1435	+	80	0	225	—	Aug.	3100
Soejarto 1484	+	85	0	150	—	Aug.	3000
Soejarto 1491	+	93	0	164	—	Aug.	3000
Soejarto 1045	+	80	0	150	—	July	3600
Soejarto 1508	+	92	0	127	—	Aug.	3000
Soejarto 1474	+	88	0	149	—	Aug.	3000
Soejarto 1335	+	40	0	240	—	Aug.	3200
Soejarto 1473	+	96	0	145	—	Aug.	3000
Fajardo G. 81	+	96	0	125	—	Apr.	3400
I. F. Holton 23	+	97	0	—	—	Jan.	3000
Cuatrecasas 20997	+	98	1	145	—	Apr.	3000
Hitchcock 20888	+	—	1.5	150	—	Aug.	3400
L. Uribe Uribe 5328	+	90	0	160	—	July	3100

FIGURES 5–8. Graphic representation of the distribution of long- and short-styled forms represented by herbarium collections, together with histogram distribution of the stamen numbers. FIG. 5, *Saurauia bullosa* Wawra; FIG. 6, *S. brachybotrys* Turcz.; FIG. 7, *S. Humboldtiana* Busc.; FIG. 8, *S. excelsa* Willd. Sample examined for each species consists of short- and long-styled forms in more or less equal numbers.

styled condition, and between high pollen fertility and a short-(obsolete-) styled condition. This correlation breaks down in *S. omichlophila*, where both long- and short-styled plants have high pollen fertility. Plants of each type occur in approximately equal numbers within a sampling collection of each species, which may reflect the distribution in the natural populations. Another significant correlation is that specimens bearing fruits have been recorded only from plants with long styles. This is cer-

tainly not mere coincidence, since all eight species discussed here (and many others for which statistics are not included) show this condition throughout. Morphological examinations from free hand sections of advanced ovaries in short-styled flowers show that these are aborted and they simply "do not grow" (PLATE II, FIG. 19). In long-styled flowers fruiting is accompanied by good seed set, except in several individuals where seed set is poor, notably in *Soejarto 1043* (*S. tomentosa*).

Short or long condition of the styles is not in any way correlated with high or low number of the stamens. As is obvious from FIGS. 1–8, and from TABLES 1 and 2, the distribution of the stamen number is continuous throughout the population, regardless of the style length. From the measurements of flower parts (data not included here), it also appears that a short- or long-styled condition is not correlated with the size of the flowers.

From field observations and from herbarium records, there is no indication of any particular flowering and fruiting season among the South American species of *Saurauia*. Flowering is usually associated with the wet months of the year. In most species, however, flowering and fruiting are continuous throughout the year, although fruiting is recorded in the herbarium collections (at least, in the eight species under discussion) only from February through October.

Pollen grains (PLATE I). All eight species have 3-colporate pollen, which is oblate spheroidal (cf. also Erdtman, 1952). Several individuals of *S. excelsa* have 3-colpate, prolate pollen grains. Most of the South American species that I have examined have oblate spheroidal pollen grains, although occasional prolate pollen is also present. No single pollen shape is restricted to a particular species. This condition applies only to fertile pollen grains, where the cell content stains uniformly with cotton blue and appears light to dark blue with bright-field illumination. The cell wall is smooth, with no observable wall sculpturing (at least with the present processing technique). The (fertile) pollen grains are binucleate at the time of anthesis (PLATE I, FIG. 14; cf. also Brewbaker, 1967); the generative cell is ellipsoidal or spindle-shaped, and the vegetative cell is roundish. The vegetative cell usually does not take acetocarmine stain so well as the generative cell. The binucleate condition of the grains may be seen (with cotton blue stain) in a sufficiently mature flower bud, prior to anthesis, and *it is assumed that this condition indicates that the pollen is fertile.*

The sterile pollen grains, on the other hand, have no fixed shape or any orientation. They may be lenticular, roundish or simply irregular in shape, but, lacking contents, do not stain. The cell wall usually is shrivelled. Some roundish pollen grains have minute dark granules within.

The size of the pollen varies, and no serious attempt has been made to measure size variation species by species. I am convinced, however, that pollen size is not taxonomically significant. Pollen size variation is always present in any preparation from a single plant, and size variation

between species is very slight. According to Erdtman (loc. cit.) the pollen size of *S. Prainiana* Busc. from Perú is 18.5 × 20 microns (oblate spheroidal), and that of a species from Bolivia identified as *S. brachy-botrys* Turcz. (probably a misidentification, since *S. brachybotrys* occurs only in southwestern Colombia) is 19 × 15 microns (subprolate). According to my rather crude measurements, fertile pollen grains vary in diameter from 15 to 25 microns, and sterile grains vary in diameter from 10 to 30 microns. There are no visible differences between fertile pollen grains from a short-styled plant and those from a long-styled plant; nor between sterile pollen grains from a long-styled and from a short-styled plant.

Androecium and gynoecium (PLATE II). There is no pollen dimorphism in *Saurauia*, in the sense of two types of pollen grains differing morphologically and correlated with floral dimorphism. The correlation in most cases is straightforward: *long styles* and *low pollen fertility* (*absolute sterility*) vs. *short styles* and *high pollen fertility*. The term *long* used here is relative, depending on the individual species involved. Species with large flowers (3–5 cm. in diameter), such as *S. bullosa* and *S. tomentosa*, have *long styles* 5–7 mm. long, and *short styles* 1–2.5 mm. long, whereas species with smaller flowers (0.5–1 cm. in diameter), such as *S. pseudoleucocarpa* Busc. and *S. micayensis* Killip, have *long styles* 3–5 mm. long, and *short styles* 0.5–1 mm. long. Styles less than 0.5 mm. long are considered to be obsolete.

The ovary of the American species of *Saurauia* is mostly five-carpellate, but in some species, e.g. *S. yasicae* Loes., *S. peruviana* Busc., and *S. leuco-carpa* Schlecht. may be three- to five-carpellate or, in *Saurauia* sp. (a new species from Bolivia to be described by me), five- to seven-carpellate. Each style of the long-styled flower is surmounted by a capitate stigma. The stigmatic surface is either roundish or cordate (1–2 mm. broad in *S. bullosa*), covered by minute papillae. The size of the stigma — and for that matter of all other floral parts — varies with the size of the flower. At the time of anthesis, the stigmas turn dark brown and become sticky. This condition lasts, in *S. bullosa*, for four to seven days. On the other hand, the styles of a short-styled flower are tipped by simple stigmas which are non-papillate, and according to my field observations, there is no change in color or stickiness during anthesis.

Pollination. It appears from field observations that pollination in *Saurauia* is promiscuous. Most flowers have persistent green sepals and white petals (free for most of their length, but coherent at the base, falling as a unit with the stamens [2]). Occasionally, some species (e.g. *S. iso-xanthotricha* Busc.) have both white and pink flowers, but I have never seen species with only pink flowers.[3] The stamens, with white filament and

[2] As a result, flowers examined after anthesis are often described as "unisexual."

[3] *S. Conzattii* Busc. from Mexico has red, beautiful flowers (Schultes, personal comm.).

yellow anthers, characteristically form a yellow clump at the center of the corolla. The anthers consist of two thecae, versatile and extrorse at the time of anthesis; the point of attachment of the filament is at the junction of the two thecae, which fork in most cases about two-thirds the distance from the (embryonic) base. The versatile anthers and the pale, morphologically unspecialized flowers represent, in a way, an adaptation for wind pollination.[4] There is no definite nectary present in the flower, but nectar-secreting tissue is found inside at the base of the corolla, partly hidden by the stamens (cf. Brown, 1935); also, most flowers have a faint, sweet scent, which in some species, especially *S. omichlophila*, is moderately strong.[5] These two characteristics suggest adaptation for insect pollination. I have found hymenopterans and other insects visiting flowers of *S. peduncularis*, *S. omichlophila*, *S. brachybotrys*, and *S. chiliantha* R. E. Schultes.[6]

Fruit and seed dispersal. The fruit of *Saurauia* is a berry filled with numerous small seeds embedded in a mucilaginous pulp. The color of the fruit is green, even when mature, although sometimes there is a purple to purple-red tinge on the green, glabrous pericarp. The sepals are persistent, as are the styles. Maturity of the fruit is indicated by an abundance of mucilage, which is rather sticky, clear, sweet and edible. Dehiscence of the fruit is septicidal along the longitudinal sutures, the septa often being membranaceous; the central column and the septa remain intact after dehiscence. In *S. bullosa*, dehiscence may occur from one to three days after a ripe fruit is detached from the tree (faster when conditions are wet) with little mechanical stimulation. The dehiscence lines start at the apex of the fruit and run gradually towards the base, at the same time discharging, or more precisely, exuding the mucilage which includes the seeds. This is, I believe, the way that the seeds are dispersed naturally, aided by the rain wash. Dispersal by birds certainly is not uncommon. Birds have been seen frequently feeding on *Saurauia* fruits (common name: *moquillo* or *dulumoco*, referring to the mucilage of the fruit). However, the effectiveness of bird dispersal must be further investigated. In all probability, diaspores may not be transported great distances in *Saurauia*; survival is insured by an abundant production of the seeds.[7]

[4] Pollen of wind-pollinated plants is usually characterized by simplicity of structure, and by the small size of the grains (between 20–60 microns, cf. P. Echlin, Sci. Amer., Apr., 1968); such is the case in *Saurauia* species.

[5] *S. aromatica* R. E. Schultes and *S. narcissifragrans* R. E. Schultes were given their epithets because of the strong and heavy scent of their flowers.

[6] L. Uribe Uribe (no. *2888*) has observed numerous bees visiting the flowers of *S. Stapfiana* Busc.

[7] The seeds of *Saurauia* are usually minute, areolate, dark brown; the testa is fragile (cf. PLATE I, FIG. 21). That *Saurauia* seeds are viable for relatively long periods is evident from the following notes. *S. kegeliana* Schlecht. (1836) was "described from living plants at Halle, Germany, that grew from seeds in soil found about the roots of plants imported from Guatemala" (note by Standley & Steyermark, Fieldiana 24(6): 431. 1949). *S. spectabilis* Hook. (Bot. Mag. 69: *pl. 3982*. 1842) was described from a "plant raised by Mr. Knight, of the Exotic Nursery, King's Road,

Geographical distribution. The center of distribution of *Saurauia excelsa* lies in the Venezuelan Cordillera de Mérida, while that of *S. Humboldtiana* is found in the Cundinamarca region, Cordillera Oriental of the Colombian Andes. There is an overlapping of range between these two species in the Santander region. *S. ursina* is centered in Antioquia, along the Cordillera Central, and its range overlaps that of *S. Humboldtiana* and, perhaps, that of *S. excelsa* as well. *S. brachybotrys* centers in the Cauca-Valle region, between the Cordillera Central and Occidental, but its range extends north to Antioquia, and south to the Nariño-Putumayo region. The Nariño-Putumayo area is located near the Colombian-Ecuadorian frontier, where the species concentration of the genus is highest. *S. bullosa*, *S. tomentosa* and *S. omichlophila* have their centers of distribution in this region also. *S. bullosa* and *S. tomentosa* have the broadest ranges of the South American species. *S. putumayonis* occurs in the Putumayo region, along the Cordillera of Portachuelo.

The four species, *Saurauia excelsa*, *S. Humboldtiana*, *S. ursina*, and *S. brachybotrys* are not effectively isolated from one another geographically or altitudinally. Although *S. bullosa* and *S. tomentosa* overlap geographically with other species, they are effectively isolated from the others altitudinally and are themselves frequently sympatric in their distribution, geographically, ecologically, and altitudinally. *S. omichlophila* and *S. putumayonis* are effectively isolated from the others, particularly ecologically, and they are spatially allopatric.

Cytology. I have examined the meiotic chromosomes of seven of the eight species under discussion: *Saurauia bullosa*, *S. brachybotrys*, *S. Humboldtiana*, *S. tomentosa*, *S. omichlophila*, *S. putumayonis*, and *S. ursina* (Soejarto, 1969). Chromosome behavior at meiosis in these species appears to be normal, and the chromosome size and morphology are remarkably stable. The haploid chromosome number of all seven species is $n = 30$. Cytokinesis is of a simultaneous type, and the tetrad arrangement is tetrahedral. Chromosome counts were all made from pollen mother cells.

DISCUSSION

In *Saurauia*, at least among the species from South America, two kinds of flowers can be distinguished. The differences lie in the size and morphology of the styles, and in the degree of pollen fertility. Anther height and pollen size and morphology appear to be fixed. It is for this reason, perhaps, that the existence of floral dimorphism in *Saurauia* has passed unnoticed for so long. Most workers on this group considered a short-styled condition to be peculiar to a particular individual or species,

Chelsea, England, from seeds imported from the Republic of Bolivia, in 1838." However, I have attempted several times to germinate *Saurauia* seeds for cytological studies without success.

or a sign of immaturity, and apparently did not appreciate the biological significance of their observations. The present study shows that floral dimorphism does exist in *Saurauia*, but that this type of dimorphism is *not* distyly or heterostyly in the true physiological sense of the word, since it appears (at least now) that no incompatibility system is involved. Low pollen fertility (to complete sterility) in a plant with long-styled flowers, and high pollen fertility in a plant with short-styled flowers is a mechanism that promotes outcrossing. In this respect, the flower of *Saurauia* must be described as *functionally dioecious*. The short-styled form with high pollen fertility may be considered a functionally staminate plant (the pistil being nonfunctional), while the long-styled form with low pollen fertility (to complete sterility) is a functionally carpellate plant (the stamens being nonfunctional). For those individuals, particularly populations of *S. omichlophila*, which are truly hermaphroditic (TABLE 2; hermaphrodites are characterized by a long-styled flower with pollen fertility 80% or more) within the dimorphic populations, further investigation is needed to demonstrate whether any self-compatibility between the pollen and the stigma of the same flower exists. From the pollen size and morphology, there seems to be no reason why it should not occur. If this is the case, species like *S. omichlophila* must be described as *androdioecious*.

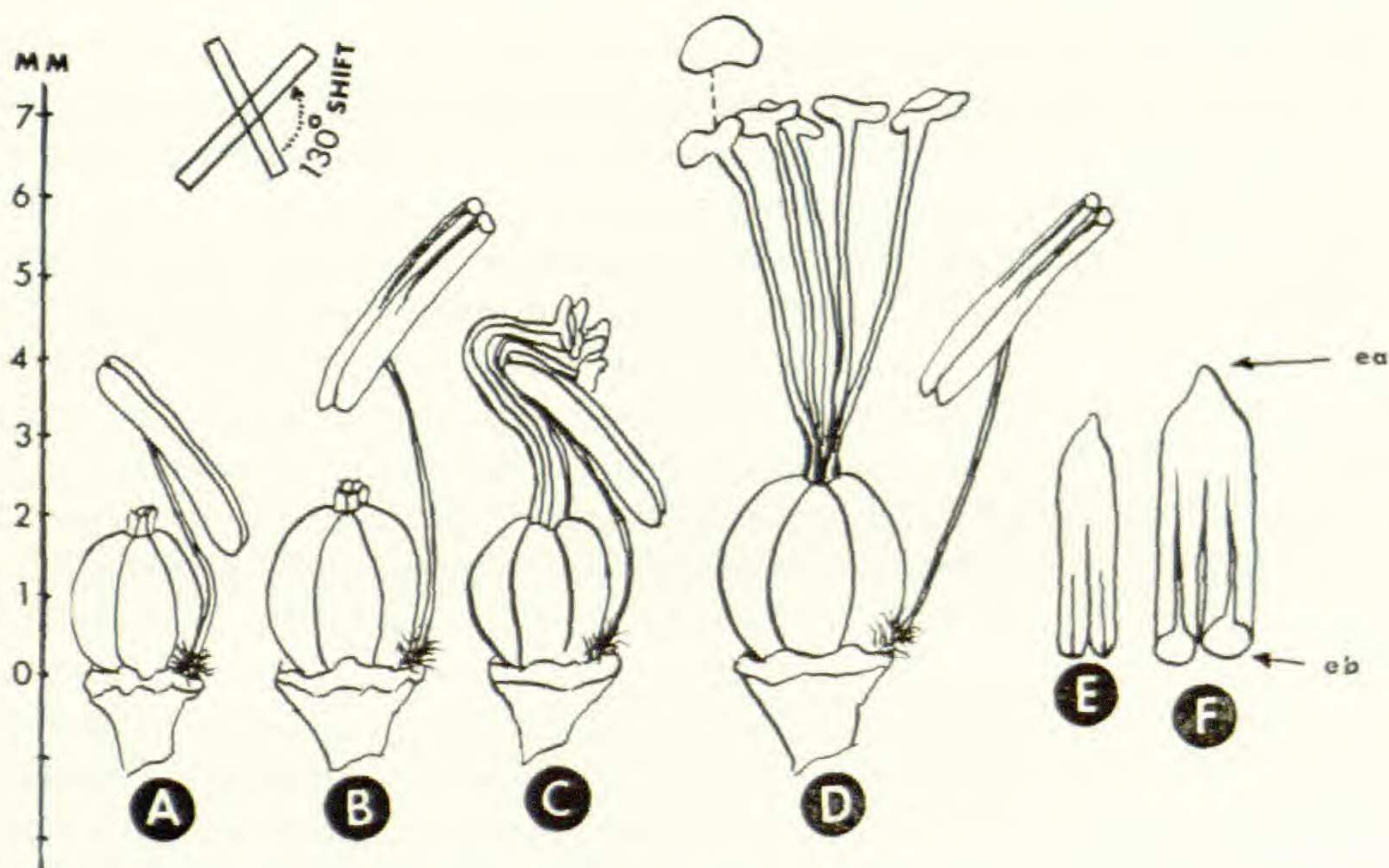The widespread occurrence of functional dioecy, an outbreeding sys-

FIGURE 23A–F. Anther orientation in the flower of *Saurauia Humboldtiana* Busc. Sepals and petals removed to show details. A, short-styled form, bud stage; B, short-styled form, at anthesis; C, long-styled form, bud stage; D, long-styled form, at anthesis; E, anther, bud stage; F, anther, at anthesis. As a result of the shift of the anther position at anthesis (approx. 130°), the anthers are extrorsely oriented. ea, embryonic apex of anther; eb, embryonic base of anther.

tem, is further enforced by the peculiar anther orientation during anthesis in the American species of *Saurauia* (FIG. 23, A–F). The end of the anther (the embryonic base) is directed away from the center of the flower as it opens, and the anther rotates about 130° on the filament so that the pollen discharge is directed away from the stigmas. Pore openings and dehiscence of the anther start at the embryonic (morphological) base and "zip" ventrally about two-thirds the length of the thecae. My field observations of this dehiscence and reorientation of the anther during anthesis are confirmed by Hunter's (1966) interpretation, from histological observations of the vascular trace of the stamen (Hunter interprets the reorientation of the anther at anthesis as 180°, with which I cannot agree). Therefore, in individuals which are truly hermaphroditic, like those in *S. omichlophila*, self-pollination is averted as much as possible. Prevention of self-pollination among the hermaphrodites is indicated by the position of the stigmas which is well above the surface of the androecium. Nevertheless, the chances of self-pollination are rather good.

From an evolutionary point of view, the immediate consequence of outbreeding is its capacity for genetic recombination to produce variability for the action of selection and other external forces which direct the evolution of populations (Stebbins, 1950). The greater part of the genotypic variation within a cross-breeding population is due to segregation and recombination of genic differences which have existed in it for many generations. As a result, in a comparable environment, the outbreeders may show great, more or less continuous, morphological variation, which is an expression of genetic variability from plant to plant. Most species populations of *Saurauia*, those which are functionally dioecious, are characterized by this type of morphological and environmental continuity. Because of a low selective pressure, variability *within* a population tends to obscure any clear-cut distinction *between* populations. The situation is further confounded by a more or less free gene flow between species populations, due to an incomplete isolating mechanism: spatial, ecological, ethological or, perhaps, genetical; this last mechanism must be further investigated. The lack of a complete genetic barrier is demonstrated by the frequent occurrence of natural hybridizations where two or more species populations are in contact or where they are sympatrically distributed. I have collected several natural hybrids of *Saurauia* from southwestern Colombia, where the greatest concentration of species is located, and the hybrid status of at least four of these plants has been confirmed by meiotic irregularities of the chromosomes (Soejarto, unpubl.). Although altitudinal isolation is usually effective, nevertheless some population contact is always present. There seems to be no effective barrier against interspecific pollination in most cases, which is reflected in the relatively uniform floral morphology. Only size variation of the flower, which is conspicuous, exists within as well as between species. Correspondingly, selective pressures are relatively weak at the stage of flowering and also at the fruiting, or dispersal stage. On the chromosome level, the differences between species populations appear to be even less significant; that is, as far as

Table 2. Saurauia omichlophila R. E. Schultes

COLLECTOR	FL. BUDS OR FLS.	POLLEN FERTILITY (%)	STYLE LENGTH (mm.)	STAMEN NUMBER	FRUIT	COLLECTING DATE	ALTITUDE (m.)
Soejarto 1493	+	90	5	18	+	Aug.	2900
Core 1019	+	95	5	30	+	July	2700
Soejarto 1176	+	90	4.5	28	+	July	2500
Soejarto 1046	+	96	4	14	+	July	3200
Soejarto 977	+	—	4.5	—	+	July	3000
Soejarto 1511	−	—	4	—	+	Aug.	2800
García-Barriga 13023	+	85	4	21	−	July	2800
L. Uribe Uribe 3876	+	98	4	25	−	Sept.	3000
Soejarto 1501	+	90	0	23	−	Aug.	3000
Soejarto 1509	+	88	1.5	20	−	Aug.	3100
Schultes 3236	+	95	0	26	−	Feb.	3200
Schultes 7560	+	90	0.5	26	−	March	2900
Core 1018	+	96	0.5	37	−	July	2700
Schultes 7560A	+	88	0.5	27	−	May	2900
Soejarto 1502	+	85	0.5	29	−	Aug.	3000
Hernández 79	+	95	0	22	−	—	3000
Soejarto 1598	+	95	0	20	−	Sept.	3000
Schultes 20098	+	92	0	21	−	June	2800
Schultes 7550	+	85	0	21	−	June	3000
Schultes 7771	+	90	0	26	−	June	3000
Soejarto 914	+	0–80	0	21	−	July	3000

my present investigations on the cytology of the South American *Saurauia* show. The inevitable consequence of all this is the difficulty of drawing clear-cut boundaries between species populations, and, consequently, in the delimitation of the species within the genus. It is unfortunate that species of *Saurauia* are unfavorable subjects for garden experiments because of climatic intolerance, poor seed germination, the large size of the plants and the length of time before they reach the flowering stage. These drawbacks, however, should not discourage workers on the group from continuing their efforts. There are several other things that can and must be done; one of these is more vigorous field work and collecting of herbarium material. The more herbarium collections accumulate, the better we can evaluate and analyze the limits of variation within and between species. Considering the relatively young age of the group, Tertiary (Eocene?; cf. Langeron, 1900, Hollick, 1936), it appears to me that evolutionary differentiation is proceeding in the genus *Saurauia*.

Finally, the realization that functional dioecy is prevalent in *Saurauia* may further confirm our opinion with regard to the phylogenetic relationship of the genus with the closely allied, predominantly dioecious *Actinidia*.

SUMMARY

The reproductive system(s) of the following eight South American species have been described and discussed: *Saurauia bullosa, S. brachybotrys, S. excelsa, S. Humboldtiana, S. tomentosa, S. omichlophila, S. putumayonis,* and *S. ursina.* As far as the present data show, seven of the eight species appear to be functionally dioecious, and one, *S. omichlophila,* is androdioecious. The flowers of these plants are dimorphic: a long-styled form with high pollen sterility (functionally carpellate) vs. a short-styled form with high pollen fertility (functionally staminate). Anther height is fixed, and pollen dimorphism related to style dimorphism has not been seen.

Although data have been compiled exclusively from herbarium examinations (presented here in graphic form, FIGS. 1–8), the following observations, based upon field and laboratory studies, have also been briefly described: pollen grain, androecium vs. gynoecium, pollination, fruit and seed dispersal, geographical distribution, and cytology.

The widespread occurrence of functional dioecy may be a useful guide in confirming the phylogenetic relationship between *Saurauia* and the closely allied, predominantly dioecious genus *Actinidia*. It is further suggested in the discussion, that the extensive morphological variability is the result of the outbreeding nature of the group, because the immediate consequence of outbreeding is its capacity for genetic recombination to produce variability in the action of selection and other external forces which direct the evolution of populations.

ACKNOWLEDGMENTS

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EXPLANATION OF PLATES

PLATE I

FIGURES 9–16. Pollen grains in *Saurauia*. FIGS. 9, 11, 14, 15, 16, fertile pollen; FIGS. 10, 12, 13, sterile pollen. FIGS. 9, 10, 11, 12, 13, 14, from *S. bullosa*, showing oblate spheroidal pollen grains, FIGS. 15 and 16 from *S. excelsa*, showing prolate pollen grains. All except FIG. 14 prepared from herbarium samples, stained in cotton blue; FIG. 14 prepared from anthers fixed in Carnoy's solution and stained in acetocarmine (only a generative cell clearly visible). FIGS. 9 and 10 approx. × 400, the others approx. × 1600.

PLATE II

FIGURES 17–22. FIGS. 17 and 20, long-styled flower (mature bud in FIG. 17, flower at anthesis in FIG. 20); FIGS. 18 and 19, short-styled flower (mature bud in FIG. 18, flower after anthesis in FIG. 19); all longitudinal sections. FIG. 22, upper view of the stigmas at anthesis. FIG. 21, seeds. All to the same scale as FIG. 19, and all from *S. bullosa*. FIG. 19 photographed from dried flowers (boiled and dissected), all others from material fixed in Carnoy's solution. Scale in FIG. 19 is in mm.
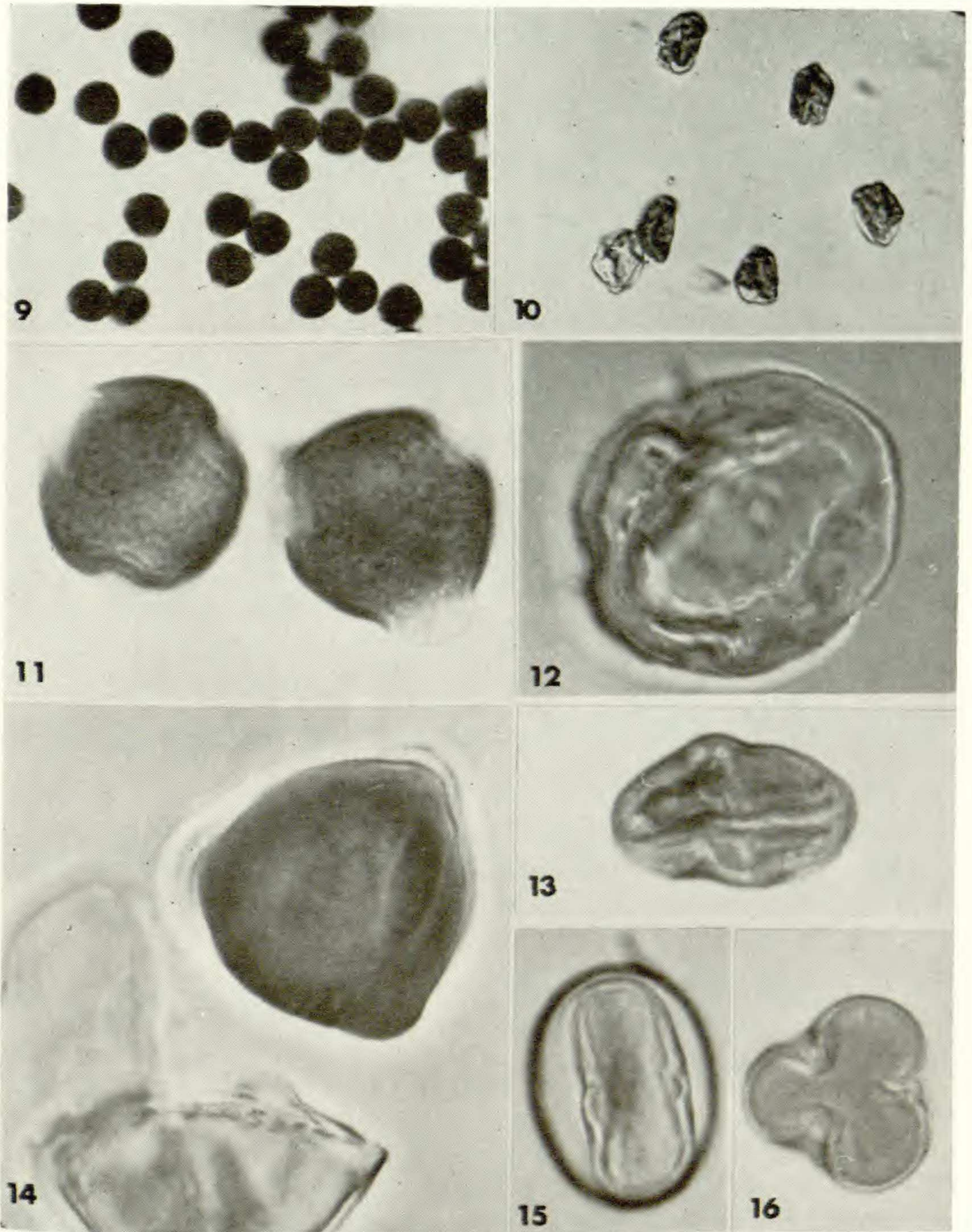
SOEJARTO, REPRODUCTION IN SAURAUIA
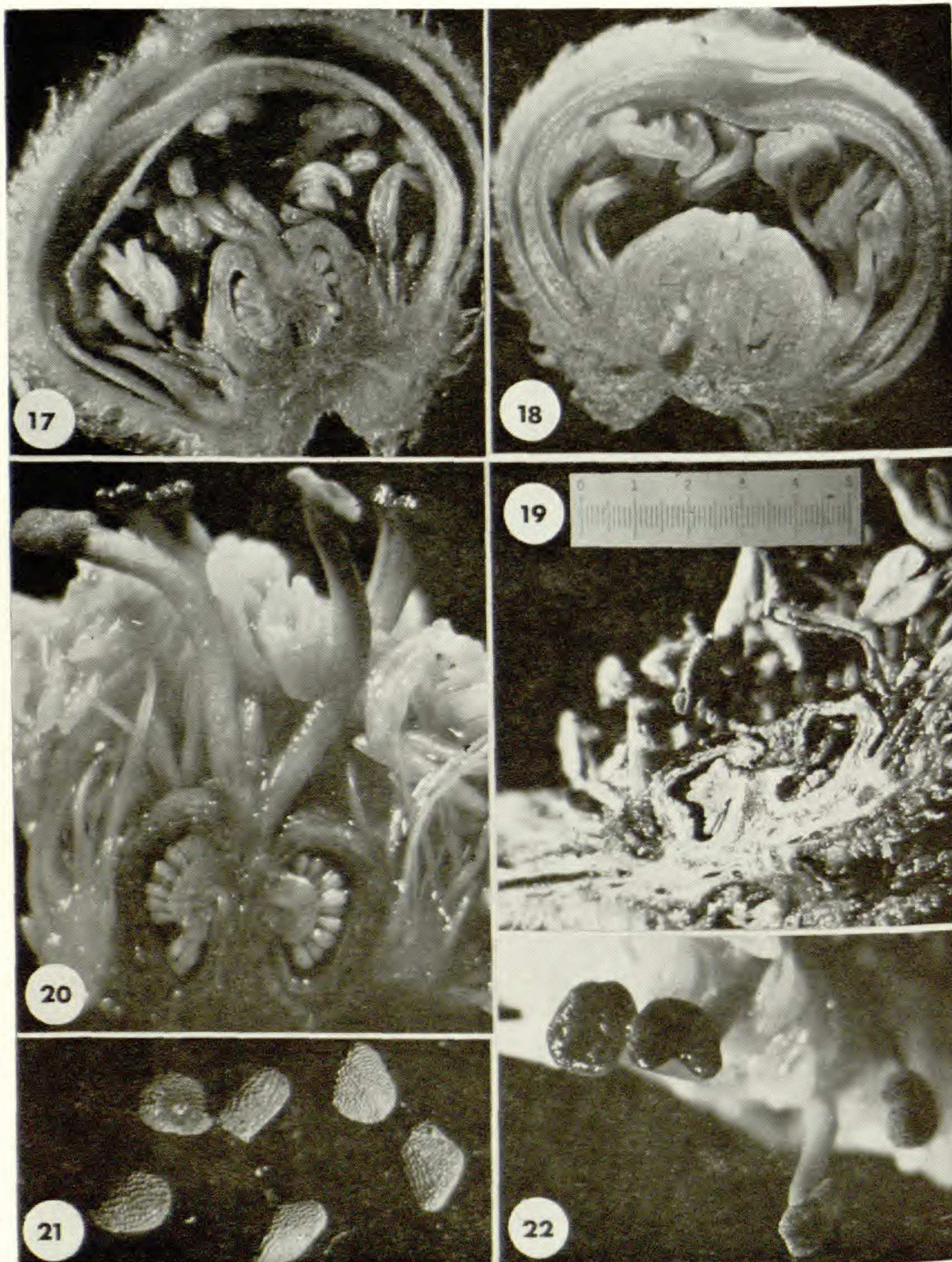
SOEJARTO, REPRODUCTION IN SAURAUIA

THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 6
AËRIAL ROOTS [1]

A. M. GILL

IN TEMPERATE REGIONS aërial roots are rare and although they may be found on a few vines they are absent from the trees and shrubs. In the moist elfin forest of Puerto Rico, however, many of the trees, shrubs, vines, and herbs form aërial roots. The tree fern *Cyathea* and the lowly *Selaginella* also form aërial roots in this environment.

Many of the aërial roots hanging freely from the plants are very characteristic of the species while some other species are difficult to distinguish by the characters of their aërial roots alone. In this study some of the distinctive characters of the roots are described and the frequency of aërial root formation on Pico del Oeste is documented.

OBSERVATIONS ON THE DISTRIBUTION OF ROOTS IN TOTO

The roots in the study area are found in four general habitats: in the soil; immediately above the soil beneath a layer of cryptogams and/or leaf litter; appressed to the trunks and branches of the trees and shrubs; and hanging freely in the air.

All the roots in the last three habitats named may be considered "aërial." Those in the second category occur in a gaseous environment immediately below the forest floor and above the soil. A mat of roots up to five centimeters thick may be formed (FIG. 1) which appears to have arisen not merely by erosion of soil but by the growth of roots out of the soil and over its surface. On steep slopes roots of sufficient rigidity may even grow through the forest floor into the atmosphere. On gentle slopes this achievement has been attained by growth along tree trunks and fallen branches beneath a layer of cryptogams and thence out to the atmosphere.

The roots of many of the vines and of the bromeliad *Vriesea* are found closely attached to rigid organic surfaces. They are often found beneath a mantle of cryptogams but are also found where such a covering is lacking. This latter type of root may also be considered "aërial" but the affinity of the roots to their supports distinguishes them from the final group which is the main subject of this paper.

The aërial roots to be considered here are those found hanging freely in the atmosphere. They arise above ground and are not closely appressed

Fig. 1. Mat of roots immediately below the litter and cryptogam layer but immediately above the soil.

to any surface. They may become anchored in the substrate and undergo considerable secondary thickening and in such cases have been termed "prop" or "stilt" roots by other authors. The aërial portions of such anchored roots may exhibit phenomena different from roots of the same species in the freely-hanging stage — those to be considered here.

Aërial Roots of the Trees and Shrubs

Many of the data pertaining to the aërial roots of the trees and shrubs of the area are shown in TABLE 1.

Origin. Aërial roots usually arise from the undersides of branches and from the main axis of the plant. They are often associated with the formation of sprouts (probably arising from dormant buds) and in such cases are found at the base of the sprout where it joins the main stem. This condition was observed in *Ocotea, Ilex, Miconia pachyphylla, Calyp-*